

Silicified Silurian bivalves from Gotland

LOUIS LILJEDAHL



Lund Publications in Geology

No. 24

LUND 1984

Silicified Silurian bivalves from Gotland

Louis Liljedahl

Doctoral dissertation at Lund university, 1984, summarizing
the following papers:

- 1983 Two silicified Silurian bivalves from Gotland. Sver. Geol. Unders. C 799, 51 pp.
- 1984a Silurian silicified bivalves from Gotland. Sver. Geol. Unders. C 804, 82 pp.
- 1984b Ecological aspects of a silicified bivalve fauna from the Silurian of Gotland. In press Lethaia, 1984.
- 1984c Janeia silurica, a link between nuculoids and solemyoids (Bivalvia). In press Palaeontology. 1984.



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ISSN 0281-1316

ISBN 91-86746-00-6

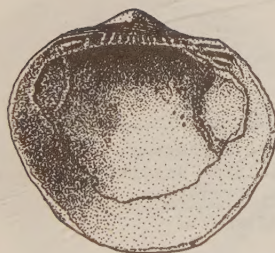
Picture on front cover is a drawing made by Claes Bergman of *Freja fecunda* Liljedahl, 1984. SGU Type 3367, sample G77-28LJ, Möllbo, Gotland.

Silicified Silurian bivalves from Gotland

av

Louis Liljedahl

fil.kand., Mlm.



Akademisk avhandling som för avläggande av filosofie
doktorsexamen vid matematisk-naturvetenskapliga fa-
kulteten vid Lunds universitet kommer att offent-
ligen försvaras i Geografiska institutionens före-
läsningssal, Sölvegatan 13, Lund, torsdagen den 17
maj 1984, kl. 10.15. Fakultetsopponent är RNDr.
Jiří Kříž, CSs. Prag.

Organization LUND UNIVERSITY Dept. of Historical Geology and Palaeontology Sölvegatan 13 S-223 62 Lund, Sweden	Document name DOCTORAL DISSERTATION Date of issue 17 april 1984 CODEN: LUNBDS/(NBGH-1008)/1-28/(1984)
Author(s) Louis Liljedahl	Sponsoring organization

Title and subtitle Silicified Silurian bivalves from Gotland

Abstract Eleven bivalve species from the Silurian (Wenlockian) Halla Beds of Gotland are treated. The state of preservation, (silicification), made possible extraction of unusually large quantities of specimens of high quality. Thus, a good picture of variation, as well as ontogenic growth series, were obtained for some of the species, making the reconstruction of the soft- part anatomy and life habits possible. These conclusions on life habits based on morphological grounds confirm the results of the ecological studies. Evidence from, for instance, population analysis, indicates that the fauna is preserved <u>in situ</u>. Several unusual phenomena, like pearl-formation, shell repair etc. were recognized. Traces of predation were observed and possible bivalve predators are discussed. Statistical treatment of the material revealed, in combination with morphological considerations, the trophic structure and a niche diversification within the sediment.
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Key words Bivalvia, taxonomy, phylogeny, anatomy, functional morphology, life habit, palaeoecology, population analysis, trophic structure, shell repair, pearl and tumour formation, predation, epibionts, bore holes, Silurian, Gotland,

Classification system and/or index terms (if any)	Sweden.
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Supplementary bibliographical information	Language English
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ISSN and key title 0281-1316 Lund Publications in Geology	ISBN 91-86746-00-6
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Recipient's notes	Number of pages 28 (+51+82+56+14)	Price SEK 25
	Security classification	

Distribution by (name and address)

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LOUIS LILJEDAHL



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Liljedahl, L. 1984 02 21: Silicified Silurian bivalves from Gotland. Lund Publications in Geology. No. 24, pp. 1-28. Lund ISSN 0281-1316, ISBN 91-86746-00-6.

Eleven bivalve species from the Silurian (Wenlockian) Halla Beds of Gotland are treated. The state of preservation, (silicification), made possible the extraction of unusually large quantities of specimens of high quality. Thus, a good picture of the variation, as well as ontogenetic growth series, were obtained for some of the species, making the reconstruction of the soft-part anatomy and life habits possible. These conclusions on life habits based on morphological grounds confirm the results of the ecological studies. Evidence from, for instance, population analysis, indicates that the fauna is preserved in situ. Several unusual phenomena, like pearl-formation, shell repair etc. were recognized. Traces of predation were observed and possible bivalve predators are discussed. Statistical treatment of the material revealed, in combination with morphological considerations, the trophic structure and a niche diversification within the sediment. Bivalvia, taxonomy, phylogeny, anatomy, functional morphology, life habit, palaeoecology, population analysis, trophic structure, shell repair, pearl and tumour formation, predation, epibionts, boreholes, Silurian, Gotland, Sweden.

Louis Liljedahl, Department of Historical Geology and Palaeontology, Sölvegatan 13, S-223 62 Lund, Sweden. 21st February 1984.

INTRODUCTION

Although bivalves are among the best known of marine inhabitants, being good ecological indicators especially for detailed, local environmental reconstructions, they are under-represented in the palaeontological literature. Silurian bivalves from Gotland are no exception, the first descriptions of which were made by Wahlenberg (1821) followed by Hisinger (1808, 1826, 1828, 1829, 1831, 1837, 1841), Lindström (1880 in Angelin & Lindström, 1888) and Philippi (1899). Munthe (1921) and Hede (1921, 1925, 1927a, 1927b, 1928, 1933, 1936, 1940, 1960) listed, Walmsley (1962) and Soot-Ryen (1964) described further species. In all, more than 60 bivalve species have been reported from Gotland, only 17 of which have been critically investigated, excluding the present silicified material. Still, the total collection of previously studied bivalves from Gotland makes up only a fraction of the available Möllbos material (also discussed in Liljedahl 1981, 1983b) and, since most descriptions are from the 19th century, they are in great need of revision.

There are a number of localities besides Möllbos yielding silicified, well-preserved fossils. Continued studies on microfossils (conodonts by L. Jeppsson and scolecodonts by C. Bergman) have contributed to the discovery of further localities with silicified fossils. Those known at present represent different bivalve communities and hence various habitats, and consequently, the possibilities of obtaining a detailed picture of the many bivalve groups of Gotland are great.

In a wider perspective examination of special bivalve occurrences, by means of classical methods are bound to give important clues to ecological enigmas of great palaeontological interest (e.g. Megalomus in enormous quantities being rock-forming at several localities in the Hemse-group and Pteronitella in mass-occurrence in the Burgsvik Beds).

SYSTEMATIC PALAEOONTOLOGY AND FUNCTIONAL MORPHOLOGY

The classification of the majority of Palaeozoic bivalves as proposed in the Treatise (Newell 1969) is provisional, the systematic position of many taxa often being based on external or insufficiently preserved features. The study of the bivalves of Möllbos exemplifies the difficulties in comparing well-preserved specimens with already named taxa whose interior is unknown. The present material is suitable as the basis for a sound classification, since also functional morphology and life habit of the taxa are considered. Comparative anatomy and population analysis of the bivalves of Möllbos suggest several different life habits at this locality.

Class BIVALVIA LINNEAUS, 1758

Subclass PALAEOOTAXODONTA KOROBKOV, 1954

Order NUCULOIDA DALL, 1889

Superfamily NUCULACEA GRAY, 1824

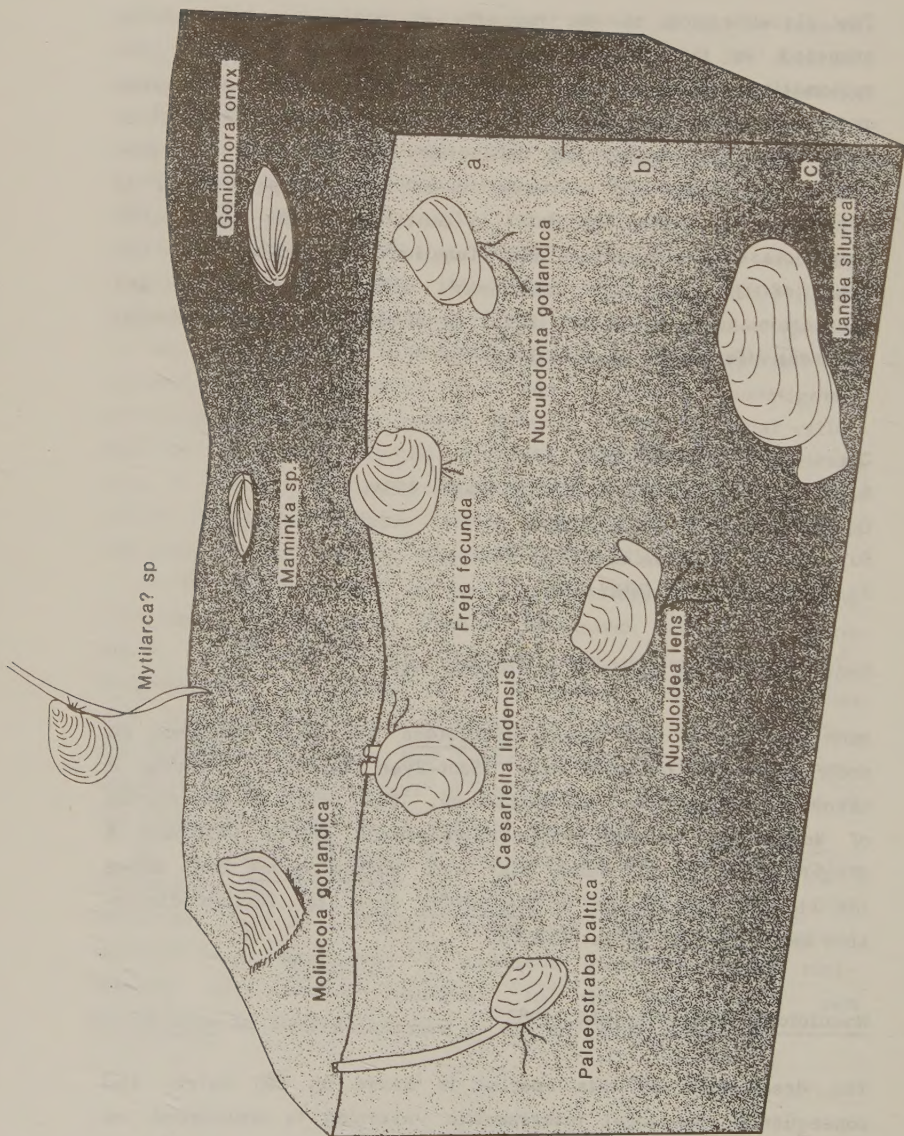
Family NUCULIDAE GRAY, 1824

Genus Nuculoidea Williams & Breger, 1916

Most species of the genus Nuculoidea are still described on their external features only (Soot-Ryen 1964:511), making a taxonomic discussion unsatisfactory. The original description of Nuculoidea includes three heterogeneous groups (Williams & Breger 1916:174) of which that with Nucula opima Hall shows the closest resemblance to Nuculoidea lens (for further discussion see Liljedahl 1983a: 26-31).

Nuculoidea lens Liljedahl, 1983

The description of this species is based on 885 valves and consequently the local interspecific variation is considered, as is also the ontogeny, since valves as small as 0.5 mm are included.



The impressions of the muscles and the anteriorly extended shell indicate a fairly large foot in N. lens (Liljedahl 1983a, Fig. 8, 1984a, Fig. 3:A; cf. Heath 1937; Driscoll 1964). Such features and a smooth shell surface are usually connected with a rapid burrowing habit (Stanley 1970:66), but the gross shell form and shell thickness is typical for a slow burrowing bivalve (Stanley 1970, Fig. 25; see also Liljedahl 1984a, Fig. 4). However, these features taken together and in combination with similarities in morphology to the extant Nucula s.s. speak in favor of an interpretation of N. lens as being a moderately rapidly burrowing, non-siphonate, protobranch deposit-feeder, probably feeding about 1-2 cm below the sediment surface (Fig. 1; see Liljedahl 1984a:10; cf. Drew 1901:314; Levinton 1977:204).

Superfamily?

Family?

Genus Nuculodonta Liljedahl, 1983

The type species and only species of the genus, Nuculodonta gotlandica, shows a number of characteristics typical for two nuculoid superfamilies (Liljedahl 1984a:6) and therefore no systematic position is proposed at the moment.

Nuculodonta gotlandica Liljedahl 1983

Nuculodonta gotlandica is represented by 1,445 valves from Möllbos, making a description similar to that of Nuculoidea lens possible. Thus, local variation in shell form and ontogeny

Fig. 1. Suggested life position of the bivalves of Möllbos. Three feeding levels (a,b,c) are distinguished within the sediment. The sizes of the shells are not relative to one another and are not drawn to scale (from Liljedahl 1984b).

are accounted for (Liljedahl 1983a:38, Fig. 14; 1984a, Fig. 1, 2). The muscular impressions of Nuculodonta gotlandica agree roughly in number and position with those of Nuculoidea lens but the adductor muscle scars are usually more deeply incised (Liljedahl 1983a:44, Fig. 15 and 17).

Functional morphology and life habit for this species are considered to be similar to those of Nuculoidea lens because of its anteriorly extended shell and the resemblance of the muscular imprints of the foot. Thus, these indicate a large foot and a moderately rapid burrowing ability (Liljedahl 1984a:11, Fig. 3:B). However, the shell of Nuculodonta gotlandica is thicker and the shell margins meet with a larger contact than in Nuculoidea lens. Furthermore, its adductor muscle scars are more heavily impressed and the hinge teeth cover about 90% of the length of the shell (70% in Nuculoidea lens). Thus, Nuculodonta gotlandica most probably occupied a life position just below the sediment surface, this species, too, being a non-siphonate protobranch deposit-feeder (Fig. 1; see Liljedahl 1984a:11).

Superfamily NUCULANACEA ADAMS & ADAMS, 1858

Family MALLETIIDAE ADAMS & ADAMS, 1858

Subfamily STRABINAE PRANTL & RŮŽIČKA, 1954

Genus Palaeostraba Liljedahl, 1984

The monotypic genus Palaeostraba is tentatively placed in the family Mallettiidae because of its similarities with the septum-bearing mallettiids Nuculites (Ordovician) and Arisaiga (Silurian) (see Liljedahl 1984a:12,18).

Palaeostraba baltica Liljedahl, 1984

Palaeostraba baltica has a smooth, thin and oval shell and is considered to be a rapid burrower (Liljedahl 1984a, Fig. 4) having lived some centimetres below the sediment surface (Fig. 1).

There are reasons to believe that Palaeostraba baltica had siphones for respiration (Liljedahl 1984a:19, 1984c). This species, constituting only 0.7% of all valves, was possibly competitively excluded by abundant non-siphonate nukuloids (constantly burrowing Nuculodonta gotlandica and Nuculoidea lens making up 70% of the valves) and Janeia silurica due to disturbance of its respiratory functions (cf. discussion in Levinton & Bambach 1975:108).

Superfamily?

Family?

Genus Caesariella Liljedahl, 1984

Caesariella lindensis (Soot-Ryen, 1964)

Caesariella is monotypic and the type species Caesariella lindensis, represented by 12 valves from Möllbos, exhibits similarities with the extant Malletia (Malletiidae in Nuculanacea) in having an external ligament and a pallial sinus, and with the Ordovician-Devonian Deceptrix (presently included in Praenuculidae in Nuculacea) in general hinge features and shell form, e.g. a truncate posterior extremity. Since Malletiidae possibly originated from Ctenodontacea (see Allen & Sanders 1969:392) the systematic position of Caesariella lindensis is difficult to establish (Liljedahl 1984a:20).

A unique feature is recorded in Caesariella lindensis, namely the possible limit of the pericardial region with heart, intestine, gonads etc. (Liljedahl 1984a:24, Fig. 12; cf. similar features illustrated in Bradshaw 1978).

The shell shape of Caesariella lindensis indicates a slow burrowing ability (Liljedahl 1984a, Fig. 4). The anteriorly expanded shell and its large accessory muscle scars suggest a large foot (active burrower), which, in combination with its thick shell and strong hinge/ligament construction, point to a life position below and close to the sediment surface (Fig. 1)

perhaps in much the same way as the similar and extant Malletia s.s. (Yonge 1941:89).

Possibly Caesariella lindensis possessed siphones, indicated by the pallial sinus. This assumption is strengthened by the fact that this species is outnumbered (its frequency being 0.3%) by non-siphonate deposit-feeders just like Palaeostraba baltica, maybe due to the same phenomena (see above).

Subclass?

Order SOLEMYOIDA DALL, 1889

Superfamily SOLEMYACEA ADAMS & ADAMS, 1857

Family SOLEMYIDAE ADAMS & ADAMS, 1857

Genus Janeia King, 1850

Living representatives of this group differ considerably from other bivalves and are therefore generally assigned to an order of their own (Newell 1969). However, a number of soft-part features suggest a systematic relationship with the protobranchs (Palaeotaxodonta = Nuculoida, in Quenstedt 1930; Yonge 1941; Allen & Sanders 1969 etc.).

The oldest known solemyoid, Janeia silurica Liljedahl, 1984, resembling both nuculoids and solemyoids (see Liljedahl 1984c), strengthens the hypothesis of a nuculoid origin of the solemyoids (cf. assumption of a common ancestor of both groups in Allen & Sanders 1969; Morris & Fortey 1976).

Janeia silurica Liljedahl, 1984

Janeia silurica, is represented by 597 valves from Möllbos. When reconstructing the soft part anatomy and life habit of this species, one must consider its intermediate morphology between the two groups mentioned. However, the life habit of Solemya, the best-known solemyoid, is poorly understood and has been considered intermediate between deposit- and suspen-

sion feeding (Yonge 1941 and others). Some students have even regarded Solemya as a suspension-feeder (e.g. Stanley 1970). However, the gut of most species of Solemya is extremely reduced in size, some species even lacking gut completely (Reid & Bernard 1980). The recent discovery of procaryotic symbionts in Solemya velum (Cavanaugh et al. 1981) may explain the enigmatic life habit of Solemya and its Y-shaped domicile (suggestion by L. Jeppsson).

Similarities to the extant Solemya and to the nuculoids indicate that Janeia silurica was a fast-burrowing deposit-feeder, being more active than the stationary Solemya (Liljedahl 1984a:35; 1984c; see also Pelseneer 1891; Drew 1900; Heath 1937; Yonge 1941; Stanley 1970). Possibly Janeira silurica lived in symbiosis with chemo-autotrophic bacteria, as does Solemya velum, which made it possible for it to live in a deep life position where no other bivalve could survive because of the sulphide-rich environment (sulphide occurrences indicated by early pyritizing in bivalve specimens from this locality, unpublished material).

Subclass PTERIOMORPHIA BEURLÉN, 1944

Order ARCOIDA STOLICZKA, 1871

Superfamily ARCACEA LAMARCK, 1809

Family?

Genus Freja Liljedahl, 1984

It is an arduous task to determine the systematic position of Freja. The type species Freja fecunda Liljedahl resembles cyrtodontaceans in its dimyarian, slightly prosocline shell, while its interumbonal growth, chevron-shaped duplivincular ligament and continuous hinge with teeth along the entire hinge line are typical arcacean features (Liljedahl 1984a:36).

The cyrtodontaceans (E. Ord. - E. Dev.) are generally believed to descend from the "actinodonts" and to be the origin of arcaceans, ambonychiaceans, pteriaceans and pectina-

PTERIOIDA

ARCOIDA

↑

ARCACEA

E



CARDIOLACEA

CYRTODONTACEA

G



Freja fecunda

F



"*Cyrtodonta*" *gibbosa*

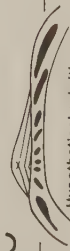
D



12

?

? C



Hypothetical primitive
ARCACEA

B



Hypothetical radical
ARCOIDA

A



"actinodonts"

ceans (e.g. Douvillé 1912, Beurlen 1944, Newell 1954, Cox 1960, Vogel 1962, Babin 1966, 1977, Stanley 1970 and Pojeta 1971, 1975, 1978). The "actinodont" hinge consists of ventrally divergent teeth, covering the full length of the hinge margin, (Fig. 2:A) in contrast to the cyrtodont hinge, exhibiting a conspicuous edentulous space between the anterior and posterior teeth (Fig. 2:D).

If the cyrtodontaceans have evolved from the "actinodonts", then there has been a reduction of the central or cardinal teeth. If then the arcaceans branched off from the cyrtodontaceans, a secondary evolution of cardinal teeth must have taken place, uniting anterior and posterior teeth and creating a continuous row of teeth in arcaceans (see Stanley 1970, Fig. 6). On the other hand, if the arcaceans branched off directly from the "actinodonts" in early Ordovician times, then there was no reduction followed by the recreation of cardinal teeth. Instead the continuous hinge teeth of the actinodonts remained in a hypothetical ancestral arcoïd (Fig. 2:B) and the "preduplivincular" ligament of the latter evolved into a true duplivincular ligament in a hypothetical primitive arcacean (Fig. 2:C; cf. suggestion of polyphyletic origin of the duplivincular ligament in Pojeta 1978). Duplivincular ligament and continuous hinge teeth are present both in Arcacea (e.g. the Ordovician Paralellodon antiquus Barrois and the Silurian

Fig. 2. Suggested arcoïd phylogeny. Unbroken lines are based on fossil evidence, broken lines are hypothetical. A. Actinodonta naranjoana (de Verneuil & Barrande), left valve (reversed here), Arenig (L. Ord.), from Babin 1966:230, Fig. 59:6. B. Hypothetical radical arcoïd assumed to have had straight hinge line, continuous dentition and "preduplivincular" ligament. C. Hypothetical primitive arcacean with straight hinge line, continuous dentition and true duplivincular ligament. D. Cyrtodonta grandis Ulrich, left valve (reversed here), L. Silurian, from Ulrich 1897:547, Fig. 43:g. E. Paralellodon rugosum (Buckman), right valve, M. Jurassic, from Arkell 1930:299, Fig. 1. F. "Cyrtodonta" gibbosa Salter BM(NH) L49858, left valve (shell, teeth and sockets reversed here), L. Silurian, also illustrated by Hind 1910, Pl. 4:17 and Vogel 1962, Pl. 51:3. G. Freja fecunda Liljedahl, 1984, SGU Type 3367, right valve, Wenlockian (Late Silurian). (Modified from Liljedahl 1984a)

"Cyrtodonta" gibbosa and Freja fecunda Fig. 2:F and G, respectively, herein; see also Liljedahl 1984a:45, Fig. 20), and in Pterioidea (e.g. the Silurian Pteronitella retroflexa in Liljedahl 1984a:54, Fig. 25). A common origin of Arcoida and Pterioidea has also been suggested on morphological and microstructural grounds (Thomas 1978:336; Pojeta 1978:237; Carter & Tevez 1978:371, 372, Fig. 6; cf. Waller 1978:359, Fig. 2).

Possibly the cardiolaceans (E. Sil. - L. Sil.), too, evolved from the arcaceans (Fig. 2) sharing a common ancestor with the two Silurian taxa mentioned (Kříž 1979:26, 37).

Freja fecunda Liljedahl, 1984

Juvenile specimens of Freja fecunda show typical free-burrowing features, while adult shells indicate byssal attachment (Liljedahl 1984a:47, Fig. 22). Thus, this species changed its life habit from free-burrowing in the juvenile stage to being endo-byssally attached when adult (Fig. 2; see also discussion in Liljedahl 1984a:48 of phylogenetic aspects on assumed intermediate life habit of Freja fecunda between free-burrowing infaunal Ordovician forms and younger semi-infaunal endo-byssate and epibyssate ones).

Order PTERIOIDA NEWELL, 1965

Suborder PTERIINA NEWELL, 1965

Superfamily AMBONYCHIACEA MILLER, 1877

Family AMBONYCHIIDAE MILLER, 1877

Genus Mytilarca Hall & Whitfield, 1869

Mytilarca? sp. Liljedahl, 1984

Mytilarca? sp. agrees in a number of diagnostic characters with Mytilarca, the best-known of the Palaeozoic genera with a concentric growth-striae ornamentation. The shell of Mytilarca? sp. exhibits adaptations for epibyssal attachment (Fig. 1)

namely a large area in contact with the substratum, maximum breadth close to the substratum, pronounced anterior reduction and a byssal opening (Liljedahl 1984:49, 50, Fig. 24).

Superfamily PTERIACEA GRAY, 1847

Family PTERINEIDAE MILLER, 1877

Genus Molinicola Liljedahl, 1984

Due to inferior preservation caused by their epifaunal life habit, seldom allowing internal features to be observed, shells of pterineids are usually difficult to classify. Most species are referred to the genus Pterinea Goldfuss or Avicula Klein (see Billings 1874:141; Williams 1908; Williams & Breger 1916:-178-179).

Billings (1874) described three new species which he incorrectly considered congeneric with Avicula retroflexa (Wahlenberg), type species of Billings' new genus Pteronitella. However, these three species differ considerably from Pteronitella retroflexa (the interior of which was first described in full by Walmsley 1962) and were excluded from Pteronitella and referred to Molinicola (in Liljedahl 1984a:53-55; see also Walmsley 1962).

Molinicola resembles Pteronitella in external characters but differs from it in having an entirely different hinge (Liljedahl 1984:55, Fig. 25).

Molinicola gotlandica Liljedahl, 1984

The ontogeny of Molinicola gotlandica, type species of the genus, is known in some detail (Liljedahl 1984a:58, Fig. 27 showing a continuous hinge in juveniles) and indicates, in combination with the duplivincular ligament, a phylogentic relationship between the pterioids and the arcoids, suggesting a common origin for both groups (Fig. 2; see also discussion on Freja).

The gross shell shape with an anterior reduction and a posterior enlargement of the shell, the inequivalve condition, its shell sculpture, a byssal opening and a strong byssal retractor muscle scar, indicates an oblique, shallow, semi-infaunal endobyssate life habit for Molinicola gotlandica (Fig. 1; for further discussion see Liljedahl 1984a:62).

Subclass PALAEOHETERODONTA NEWELL, 1965

Order MODIOMORPHOIDA NEWELL, 1969

Superfamily MODIOMORPHACEA MILLER, 1877

Family MODIOMORPHIDAE MILLER, 1877

Genus Goniophora Phillips, 1848

Most species assigned to Goniophora are known from their exterior only, the diagonal keel being the most salient feature, apart from its shell form. The hinge of the type species is not known and therefore the systematic position of species now referred to Goniophora remains uncertain (Liljedahl 1984a:63-66).

Goniophora onyx Liljedahl, 1984

The proposed life habit of Goniophora onyx as shown in Fig. 1 (see also Liljedahl 1984a, Fig. 30) agrees with that of an illustrated articulated specimen in situ on a bedding plane (in Drevermann 1902, Pl. 11:4). A somewhat different life position was suggested by Stanley (1972:194, Fig. 28; for a detailed discussion see Liljedahl 1984a:72, Fig. 30).

Subclass?

Order?

Superfamily?

Family possibly ANTIPLEURIDAE NEUMAYR, 1891

Subfamily possibly ANTIPLEURINAE NEUMAYR, 1891

Genus Maminka Barrande, 1881

Maminka sp. Liljedahl, 1984

Maminka sp. is the first species of the genus with a known interior and therefore an emendation of the generic diagnosis was given in Liljedahl 1984a:73. The life habit reconstruction in Fig. 1 (reclining) is conjectured and based on the inequivalve nature of the valves.

Genus and species indeterminable

A small articulated specimen, that can not be further classified, was found. Its interior is not observable but the conspicuous concentric sculpture differs from the smooth external surface with thin growth lines in the two otherwise similar Nuculodonta gotlandica and Nuculoidea lens from Möllbos.

ECOLOGY OF THE BIVALVES OF MÖLLBOS

(This section is a summary of Liljedahl 1984b)

Palaeoecological interpretations must of necessity be based on extant biological courses of events, although the comparisons have to be made with caution. Bivalve shell form is related to the life habit of the animal (Stanley 1970) and thus fossil bivalves are excellent tools in reconstructing palaeoenvironments.

Life- or death assemblages. - The first task in palaeoecological analysis is to determine whether the fossil remains are preserved in situ or were transported into the association concerned. In most macro-fossil collections there is a conspicuous lack of small specimens. In glaring contrast to this, the silicified fauna of Möllbos comprises wide size-ranges, including juvenile bivalves 0.5 mm long, of species with 15 mm long adults. Furthermore, the exceptionally well-preserved specimens

also indicate that this bivalve fauna is undisturbed, except for post-mortem disarticulation and fragmentation of shells caused by compaction, movements by scavengers and burrowing organisms, probably mainly bivalves.

The size-frequency distribution pattern of most samples from Möllbos is polymodal and negatively skewed. Correspondence between maxima in the size-frequency diagrams of valves and growth-rings, respectively, suggests seasonal mortality, i.e. the bivalve accumulations represent life assemblages (cf. Craig & Hallam 1963:743; Craig & Oertel 1966:350, 351).

Growth rings, pathology, epibionts etc. - A number of valves of Nuculodonta gotlandica and Nuculoidea lens show thin concentric lines between conspicuous growth-stops appearing as rings on the external surface of the shells. Such features are interpreted as growth features (Panella & McClintock 1968:69; Rhoads & Panella 1970:145, 153), indicating a maximum age of about 7 years for Nuculoidea lens.

Bivalves are famous for their ability to produce pearls. Irritation caused by foreign particles induces the animal to produce excess shell material around these, thus forming a pearl (Jameson 1912; Boettger 1954; Boshoff 1968 etc.). Blister-pearls are found in two species from Möllbos, the semi-infaunal Molinicola gotlandica (4% of all shells) showing the highest rate of infestation, while only one shell of the infaunal Nuculodonta gotlandica (42%) contains a pearl. These are the oldest known bivalve pearls (see Kríž 1979:40 on Ludlovian pearls).

One valve of Nuculodonta gotlandica has a previous marginal defect indicating a formerly damaged mantle edge, probably caused by an attacking predator. The damaged mantle gradually recovered as shown by the successively changing outline until a normal ventral margin was re-established.

One valve of Nuculodonta gotlandica has a 0.8 mm long tube close to the posterior adductor muscle scar. It is attached by its base, the distal end pointing postero-laterally. Possibly it was formed or thickened by shell material secreted by the bivalve as a protection around the organism. The position of the tube, close to the discharge area of the anus of the

bivalve, suggests a commensal affinity (cf. living Polydora in bivalves, Bromley 1970:50; cf. also the Devonian commensal in brachiopods described by Chatterton 1975).

Quite a few specimens of the Möllbos bivalves contain encrusted epibionts such as tabulate and rugose corals, worm tubes, hold-fasts etc. The semi-infaunal Molinicola gotlandica and Goniophora onyx show the highest percentage of epibionts, while only one shell of the infaunal Nuculodonta gotlandica accommodates a worm tube inside its shell.

A number of bore holes, 200-300 μm in diameter, in two shells of Molinicola gotlandica, indicate the dwelling of slow-boring sedentary organisms. One of the valves contains 10 boreholes against five of which the bivalve defended itself successfully by producing surplus shell material around them. The second shell has three holes showing no signs of shell repair.

Since the producer of the holes is not found in connection with the holes and since drilled round holes are fairly uncommon in the Palaeozoic (Bromley 1981:57) one can only speculate on their origin. Gastropods, cephalopods, nematods and sponges can be considered, but predation is normally recognized by a single hole only, while groups of holes do not suggest predation but, as mentioned, indicate activity of an endolithic organism (Richard Bromley, pers. com.).

Predation. - Many predators of bivalves leave the shell of their prey intact (Carter 1968). Consequently, it is very difficult to establish whether a bivalve was attacked and consumed or died of other causes. Most probably some of the fragmentation of the bivalves of Möllbos is due to predation.

One valve contains a repaired margin, the injury probably being inflicted by an attacking predator. Another valve shows a warped outline caused either by lack of food or by the attack of a predator.

Possible predators of the bivalves of Möllbos were arthropods (trilobites, eurypterids), fish, cephalopods and asterozoans. The only fish species found at this locality, an agnathan (Doris Fredholm, pers. com.), probably feeding on organic mud, bottom detritus and plankton (Tiiu Märss, pers.

com.), could theroretically have swallowed juvenile bivalves as well. Probable predatory fish, acanthodians, were rare in the Wenlockian and have not been found in Möllbos. Asterozoans and some cephalopods, however, leave the bivalve shell undamaged after having gormandized on the animal and are thus difficult to connect with predation.

Trophic structure and niche diversification. - The bivalve fauna of Möllbos, comprising 11 species, thrived in a muddy substrate and was overwhelmingly dominated by deposit-feeders. Six deposit-feeding species (infaunal) make up almost 90% of the population, while five suspension-feeders (3 semi-infaunal, 1 reclining, 1 epi-faunal) make up only about 10%. Evidently the constantly burrowing deposit-feeders produced an unstable sediment surface of high water content, vulnerable to erosion. In such an environment, the food-gathering and respiratory organs of suspension-feeders and siphonate deposit-feeders, respectively, will be disturbed. This type of species are therefore greatly outnumbered by the deposit-feeders (Sanders 1958, 1960; Rhoads & Young 1970; Levinton & Bambach 1975; Levinton 1977).

Co-existence of the three most abundant species, Nuculodonta gotlandica (44% of all valves), Nuculoidea lens (27%) and Janeia silurica (18%) suggests niche diversification resulting in three different feeding levels within the sediment, Nuculodonta gotlandica inhabiting the shallowest, Janeia silurica the deepest (Fig. 1). The siphonate deposit-feeders Palaeostraba baltica (0.7%) and Caesariella lindensis (0.4%) are almost totally crowded out, probably due to the same phenomena described above, concerning deposit-feeders/suspension-feeders.

Palaeostraba baltica and Caesariella lindensis are lacking in the samples dominated by Nuculodonta gotlandica but are present in those dominated by Nuculoidea lens and Janeia silurica. This suggests that Palaeostraba baltica and Caesariella lindensis inhabited a different feeding niche than Nuculoidea lens and Janeia silurica, i.e. they shared the shallowest level in the sediment with Nuculodonta gotlandica (Fig. 1).

Nuculoidea lens and Janeia silurica occur together in almost equal numbers, possibly indicating an ecological relationship

similar to that between the extant Nucula proxima and Solemya velum (in Levinton 1977:208, 209, Fig. 13). It should also be noted that Nuculoidea lens and Nucula proxima are taxonomically closely related, which is also the case with Janeia silurica and Solemya velum.

ACKNOWLEDGEMENTS

Many persons have contributed and made possible this thesis. First of all my parents encouraged me during my school years, their never ceasing interest in my education having inspired me throughout. Sven Laufeld enthusiastically supported and guided me through the years and helped me as a friend and colleague in every way. Lennart Jeppsson, my supervisor, devoted a great deal of his time teaching, criticizing and suggesting, showing unlimited patience. Anders Martinsson's inspiration and help has been of the greatest importance to me. Tragically enough he did not live to see the results of his sowing. Anita Löfgren and Gerhard Regnéll read and improved all, Kent Larsson, Anders Martinsson, Jiří Kříž, Jeffrey Levinton, John Pojeta Jr. some of my manuscripts. Jan Bergström, my old teacher, stimulated my interest for palaeontology during the course of my basic studies. Jiří Kříž, John Pojeta Jr., John Allen, Claude Babin, Curt Ochelman, Richard Bromley, Brian Chatterton, Jeffrey Levinton, Christina Franzén, Peter Miles, Sven Stridsberg, Doris Fredholm and Tiiu Märss showed interest in my work and shared their knowledge in stimulating discussions. My colleagues Sven Stridsberg and Claes Bergman contributed with photographic and artistic assistance, respectively. Valdar Jaanusson, Hermann Jaeger, Noel Morris, Adrian Rushton, W.J. Norton and Vojtěk Turek gave me access to and arranged loans from various collections. Margaret Greenwood-Petersson and Karin Ryde gave linguistic help, Christine Ebner, Christin Andréasson, Inga Palmaer and Inger Lander finished my drawings and Erna Hansson, Ingrid Lineke, Evy Liljedahl and Mervi Hjelmroos typed the manuscripts.

The work was carried out at the department of Historical geology and Palaeontology, Lund and at Allekvia Research Station, Gotland. The Geological Survey of Sweden financed part of, and Project Ecostratigraphy most of my field work and travel expenses to museums. The thesis is a contribution to Project Ecostratigraphy (IGCP Accession No. 53).

Thanks are also due to Gordon Lightfoot, David Allan Coe and the Carlsberg Brewery for evening relaxation and to my constant field companion Caesar. Last but not least my wife Evy gave me kind and everlasting support and comfort and on our field trips taught me a love of birds.

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ISSN 0281-1316